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(6) # THE RESPONSE OF THE OTOLITH ORGANS TO TILT

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USAF School of Aerospace Medicine
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FOREWORD

This report was prepared in Vestibular Laboratory of the Ear, Nose, and Throat Department, by —

(19) by MORGAN E. WING~~, Major, USAF, MC~~

ABSTRACT

Action potentials and their changes in response to tilt were recorded from 60 units in the vestibular ganglion, presumably supplying the otolith organs of 10 cats. The action potentials in all units were infrequent and irregular after position was maintained for some time. The majority of the units showed no response to any change in position. In most cases, of those which exhibited a response, the responses were delayed an average of 40 seconds. The evidence presented supports the view that the utricle and saccule may be vestigial organs, or at least do not function meaningfully in the orientation of the cat with respect to the gravitational field.

This technical documentary report has been reviewed and is approved.

Robert B. Payne

ROBERT B. PAYNE
Colonel, USAF, MSC
Chief, Operations Division

THE RESPONSE OF THE OTOLITH ORGANS TO TILT

1. INTRODUCTION

There has been much recent interest and speculation regarding the function of the otolith organs, particularly the impact of space flight upon their function. The otolith organs have been considered to be the receptors for linear acceleration and for orientation of the head with respect to the gravitational field. This concept has been well demonstrated in the lower vertebrates and has never been seriously questioned in the mammal. The existing literature regarding the function of the otolith organs in the mammal is largely inferential since their function has never been measured directly.

Recording from the utricular nerve in the frog, Ross (9) describes two types of gravity receptors: (1) those responding best when the head is tilted out of the level position, and (2) those responding only when the previously tilted head is returned to level. He concluded that the majority of utricular receptors react to only one of the two directions of tilting in a given plane. Similar findings were reported by Lowenstein and Roberts (8) working with the elasmobranch. In addition, they described a resting discharge which is increased or decreased by positional changes. Adrian (1), recording from the brain stem of the cat, presumably from the vestibular nuclei, states that the gravity receptors are increasingly stimulated as the head is tilted out of its normal position. Cramer (4), recording from the same region, reported an initial transient response to tilt which rapidly adapted within 15 to 30 seconds.

Rupert et al. (10) report on the activity of vestibular neurons in the brain stem of the cat which responded to head movements. They describe units which respond to static position and to movements in one or both directions; however, it is not made clear how these responses are distinguished from proprioceptive responses which were also described in their study.

In a preliminary study, Brown (3) presented some evidence that the otolith organs may be relatively inefficient in orientation with respect to gravity when proprioceptive and exteroceptive cues are obscured.

This study attempts to measure the activity of the neurons supplying the otolith organs of the cat, directly at the vestibular ganglion, when the animal's position is changed with respect to gravity and that position is maintained for some time.

2. PROCEDURE

The cat was anesthetized with intravenous sodium pentothal. The common carotid arteries were ligated and a tracheotomy was performed. The head was fixed, and the neck, thorax, and pelvis were rigidly secured to the cat board by means of plaster of paris bandage. An opening was made in the left parietal region with a cutting burr and was widened radically with rongeurs. The forebrain was removed by aspiration, sparing the pons and medulla. The left half of the bony tentorium was removed with burr and rongeurs, and the left lobe of the cerebellum was retracted medially with a small cotton pledget, exposing the superior surface of the temporal bone. The internal auditory meatus was located, and under magnification with the Zeiss otomicroscope, that portion of the temporal bone overlying the vestibular nerve and ganglion was removed. A segment of the facial nerve in close proximity to the ganglion was excised. Bleeding was controlled with Gelfoam, cotton pledgets, and

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bone wax. Heat and other physiologic support were used when required.

The electrodes used in this study were made from ordinary sewing needles 40 to 50 mm. in length. They were electropointed to provide tips less than 3 μ and were insulated with shellac. Impedance was approximately 20,000 ohms. These electrodes were sufficiently stiff to permit minimum vibration.

The electrode was coupled to a Grass P-5 preamplifier. The amplified signal was led to a Tektronix 502 dual-beam oscilloscope and recorded on a Grass kymograph camera. Visual and auditory monitoring were used throughout the experiments.

The micromanipulator was mounted on the cat board and the electrode was driven vertically into the vestibular ganglion. The manipulation of the electrode was observed under 16 power magnification. Action potentials were readily obtained in most cases. No vigorous attempt was made to limit action potentials to those originating from a single cell. When action potentials of four or less different magnitudes were detected, advancement of the electrode was stopped. The action potentials were monitored for changes in frequency following caloric testing, fore and aft oscillation, and rotation about a vertical axis. In most cases, it was much easier to locate units which gave a prompt response to caloric testing and rotation. These responses were always consistent with those expected with stimulation of the semicircular canals. In the absence of changes in frequency, it was assumed that the electrode was recording impulses from cells supplying the otolith organs. In this event, the cat was adapted to the horizontal position. After starting the camera, the cat was tilted either nose down or nose up, and left in this position for variable lengths of time, generally 3 to 6 minutes. Following the tilt, the cat was returned to the horizontal and left for a similar length of time, then tilt in the opposite direction was carried out in the same manner. A similar sequence was followed for lateral tilt. Following these sequences, a new electrode placement was sought and the experiment was repeated, using a different order of presentation of stimuli.

During the first portion of the study, the tilt was performed manually and the cat board was propped in position, about 15 degrees from horizontal. In the remainder of the experiments, a motor-driven tilt table was used and the animal was tilted approximately 45 degrees from horizontal. No difference was noted in the response obtained by either method.

3. RESULTS

Records were obtained from 60 units in 10 cats. Any change in frequency following a change in position was considered to be a response. Owing to the relatively low frequencies encountered, they are recorded as potentials per 5-second interval. Frequencies ranged from a low of zero to a high of 79 per 5-second interval. In most cases, the peak frequencies were between 15 to 40 potentials per 5-second interval. The amplitude of the potentials varied from 100 to 500 μv.

All units, after the cat was left in position for several minutes, exhibited an irregular frequency of action potentials which appeared to be random. The intervals between potentials varied from extremes of 1 to 180 seconds, but most often from 5 to 30 seconds. No regular resting frequency was observed for any unit.

Of the 60 units, 36 exhibited no response to any direction of tilt, and the irregular, infrequent potentials continued without change. Twenty-four units showed a definite response to one or more changes in position. The 24 units responded to a total of 58 changes in position (table I). Eight of the units responded

TABLE I

Twenty-four units responding to one or more changes in position

Number of units	8	6	7	1	1	1
Number of tilts which produced responses	1	2	3	4	6	7

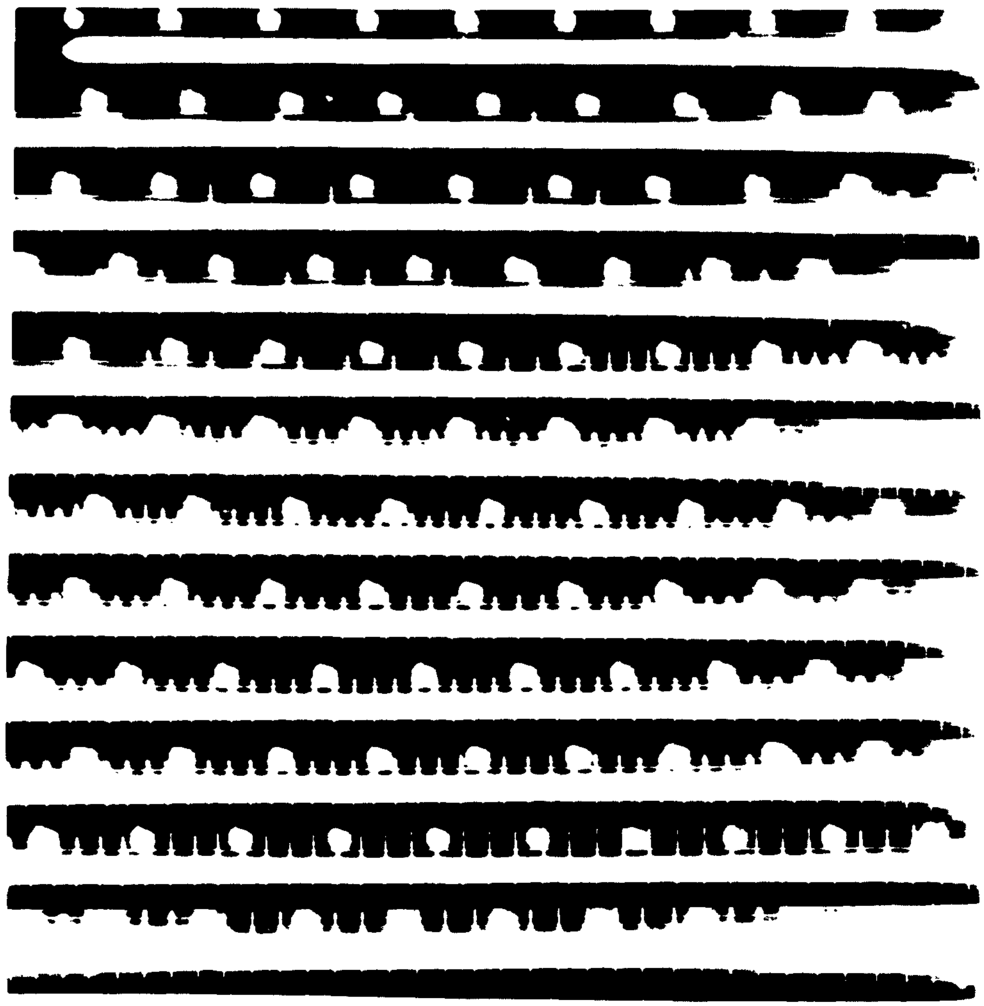

FIGURE 1

Response of a single unit during the first 118 seconds following tilt to horizontal from left lateral position. Time marker, 1 second.

to only 1 of the position changes, while 6 units responded to only 2. Seven units responded to 3 position changes and 1 unit each to 4, 6, and 7 changes in position.

Two types of response were observed: delayed and immediate. A portion of a recording demonstrating a delayed response is shown in figure 1.

The response of the same unit to a series of position changes is shown graphically in figure 2. Of the 58 tilts which produced a response, 45 were delayed and 13 were immediate. The responses may be further categorized as incremental and decremental (table II). Only 6 of the tilts produced decremental response, and in every case it was an immediate change in frequency. The minimum frequency was usually reached 20 to 30 seconds after the change in position, and this was followed by a rise in frequency which exceeded the frequency at zero time. Of the 52 tilts which produced an incremental response, 45 were delayed and 7 were immediate. The delay between stimulus and response ranged from 5 to 180 seconds, the

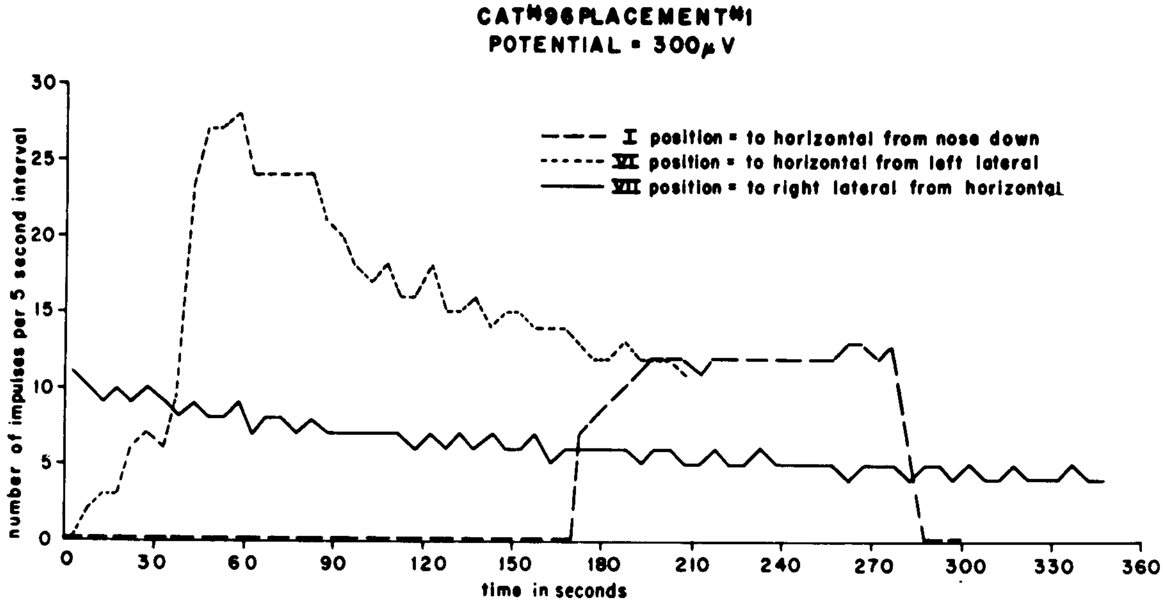

FIGURE 2

Response of a single unit to changes in positions as shown. This unit exhibited no response to the other tilts of the series.

TABLE II

Fifty-eight tilts which produced a response

	Incremental		Decremental	
	Delayed	Immediate	Delayed	Immediate
Number of tilts	45	7	0	6

average delay being 40 seconds. The immediate incremental responses generally did not reach their peak frequency until approximately 30 seconds after the tilt. An example of a unit showing an immediate response is shown in part, as recorded in figure 3 and shown graphically in figure 4. Following the peak frequency, there was a gradual decline in frequency which took place over a period of several minutes.

In a few cases, following the delay, there was a rapid rise and fall in frequency which took place over a period of approximately 30 seconds, often followed by similar smaller increases and decreases at intervals of 40 to 180 seconds, and a gradual return to the irregular infrequent potentials 5 or 6 minutes after zero time.

In only one unit were there opposite responses to opposing directions of tilt. In cat number 97, one unit exhibited an incremental response following tilt to nose up from horizontal, while tilt to horizontal from nose up and to nose down from horizontal produced a decrease in frequency.

Tilt into the horizontal position produced a response 33 times, while tilt out of the horizontal produced a response 23 times. Tilt directly to nose down from nose up without stopping in horizontal position caused a response on only two occasions.

4. DISCUSSION

The original purpose of this experiment was to study the sensory adaptation of the otolith organs. In the earlier exploratory portion of the experiment, records were obtained

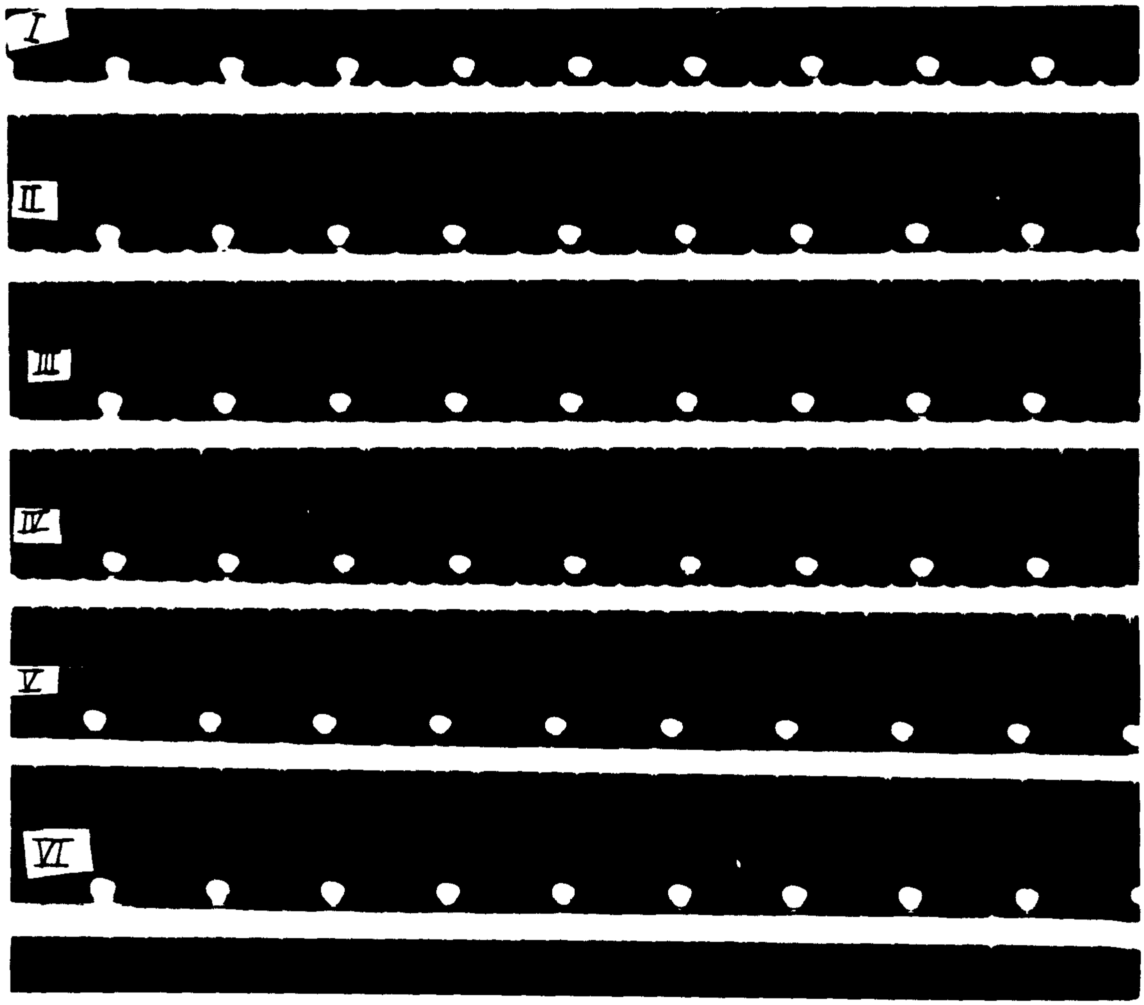

FIGURE 3

Response of 3 units at 30-second intervals following tilt to nose down from horizontal. Note that the large potentials (500 µv.) show an immediate response which does not reach its peak until approximately 90 seconds following tilt. Time marker, 1 second. I — *zero time;* II, III, IV, V, *and* VI — *30, 60, 90, 120, and 150 seconds after change in position.*

from 12 units in 4 cats. Recordings were made for several seconds at zero time, again at 1, 2, 3, and 5 minutes after tilt, and in some cases at 10, 20, and 30 minutes after tilt. The records obtained were very confusing as there appeared to be no consistency in the response and no recognizable pattern.

In the study of the 60 units — which is the basis of this paper — it was decided to operate the camera continuously during each experiment in order not to overlook any of the characteristics of the responses.

Evaluation of the recordings obtained reveals a pattern which is quite at variance with the classic concepts of the functions of the otolith organs. By far the most striking observation is the considerable delay from the onset of the stimulus to the response. Obviously the cat does not depend upon this type of response to orient his head with respect to

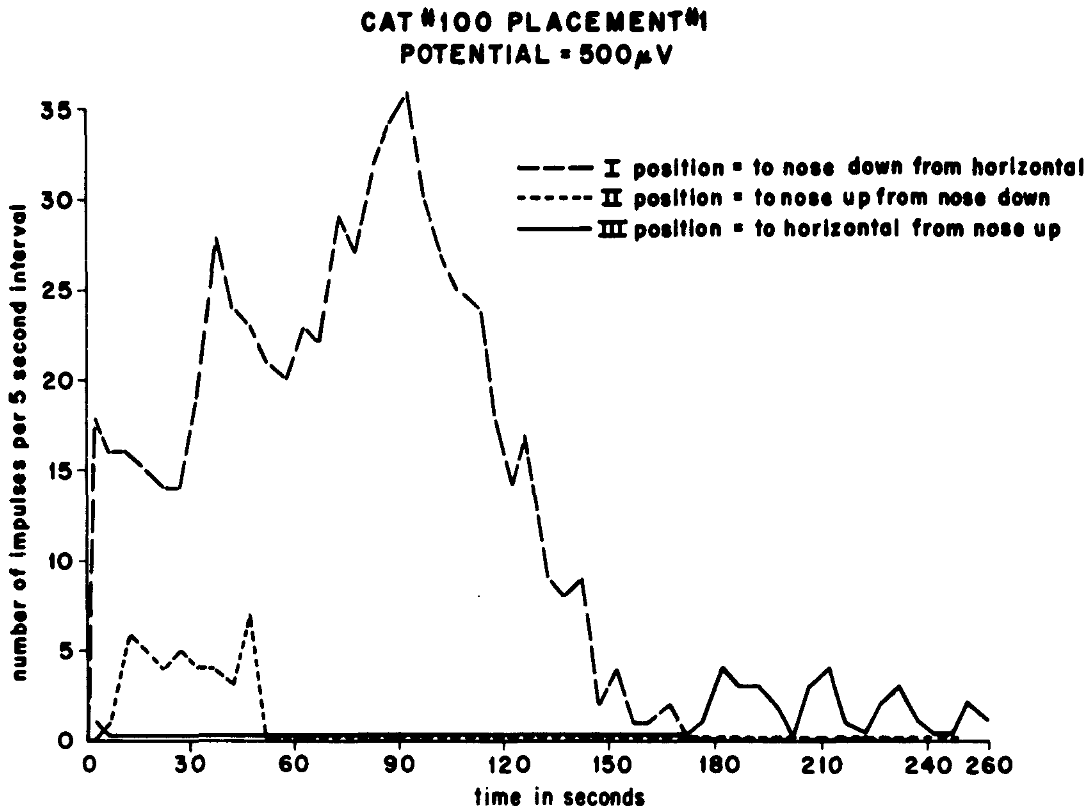

FIGURE 4

Example of a unit showing immediate response to a change in position. Note that the peak frequency was not reached for approximately 90 seconds and adaptation occurred at 150 seconds. There was no response to the other position changes except for the slight response to nose up from nose down as shown.

the gravitational field. The frequency of action potentials in many units is unchanged with tilt in any direction, which is further evidence that the otolith organs are of little importance to the static equilibrium of the cat.

The delayed response obtained in these experiments may have the same significance as the "lag time" of the oculogravic illusions as described by Graybiel and Brown (7). Reconciliation of the findings in this study with other aspects of the experiments with the oculogravic illusion (5, 6) is less apparent. Brandt (2) showed that in acquired bilateral loss of labyrinthine functions in 2 patients, the oculogravic illusion was demonstrable after a few months, although it was distorted during the acute phase of the disease. He attributes the illusion to proprioceptive and exteroceptive sensors after loss of vestibular function.

It is concluded that the utricle and saccule in the cat, and possibly in other mammals, may well be vestigial organs. It seems reasonable that functioning otolith organs are much more important to the lower vertebrates, particularly the elasmobranchs and other fishes, since their proprioceptive and exteroceptive stimuli are more likely to be somewhat obscured by their more dense liquid environment.

It seems unlikely, in view of the findings in this study, that the otolith organs will play an important part in man's adjustment to a weightless environment. His orientation will probably depend entirely upon proprioceptive and exteroceptive pathways in the absence of angular accelerations. If, in a weightless environment, centrifugal force is used to simulate gravity, then the major problem with disorientation will undoubtedly be due to the function of the semicircular canals.

The problem explored here may become extremely important in the next few years and definitely deserves more extensive investigation along the same lines explored in this study. In addition, future investigations should include the effects of linear accelerations greater than plus or minus 1 G, as well as the function of the otolith organs in aquatic mammals.

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Unclassified Report

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